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# STUDIES IN THE PHYSIOLOGY OF COMMENSALISM. 1. THE POLYNOID GENUS ARCTONOË

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Significant work on the role of specific chemical factors in controlling hostparasite or host-commensal relationships has been published by Thorpe and Jones (1937) and by Welsh (1930, 1931). The former authors have demonstrated the significance of olfactory conditioning in host-selection by parasitic insects. Welsh has shown that the normally positively phototactic sign of the mite *Unionicola* is reversed by a substance released from its host, the fresh-water clam *Anodonta*, and also that the sign of three species of *Unionicola* occurring in clam hosts of different genera can be reversed by substances from their hosts alone. To the writer's knowledge, however, no experimental work has been done on any of the legion of hostparasite or host-commensal associations to be found in the sea, nor has it been demonstrated whether or not in any of these a chemical bond exists between host and partner.

The members of the polynoid genus *Arctonoë* present an interesting commensal complex. These worms can readily be collected in Puget Sound both in the intertidal zone and by dredging; along with their hosts they are in many ways admirably suited to experimental work. In Table I the host genera of the three described species of *Arctonoë* are listed, as given by Pettibone (1947) and the Berkeleys (1948). It is to be noted that *A. fragilis* (Baird) is listed as commensal with certain starfish only, while *A. pulclura* (Johnson) and *A. vittata* (Grube) are commensal with certain starfish, holothurians, gastropods, chitons and terebellids. The records would seem to show that some hosts (see arrows) may harbor two species of commensals, though there are no records at hand of an individual host with more than one species of commensal. The cucumber *Stichopus*, although not listed as a host of *vittata* by these authors, is included on the basis of commensals identified for the writer by Dr. Olga Hartman, according to whom the commensals of *Stichopus* may show some characteristics of *pulchra* and some of *vittata*.

While some commensal populations of *Arctonoë* appear to be relatively distinct on anatomical grounds (markings, condition of neuropodial setae and margins of elytra), others are variable and appear to include intergrades. By dealing with the complex as made up of populations on certain specific hosts it seemed that it might be possible to cast some light on the basic physiology of the partnerships and thereby. incidently, on the taxonomic problems involved. The primary question arose: "How are these worms bound to specific hosts, existing as they may in environments

## TABLE 1

	fragilis (Baird)		pulchra (Johnson)		vittata (Grube)
Asteroidea	Evasterias Luidia Stylasterias Orthasterias	←→	Solaster Luidia Pteraster	$\leftarrow \rightarrow$	Solaster Dermasterias Pteraster Henricia Crossaster
Holothuroidea Gastropoda	Leptasterias Pisaster*		Stichopus Megathura*		(Stichopus) Diadora Puncturella Acmaea
Amphineura Polychaeta			Cryptochiton* Loimia*	<b>←</b> →	Cidarina Argobuccinium Cryptochiton Neoamphitrite

Hosts of the Genus Arctonoë

\* Not recorded as hosts in Puget Sound.

where other species related to their hosts but without commensals are in close association or in actual contact with them?"

To the end of determining whether some specific chemical bond exists between commensal and host, studies were conducted at the Oceanographic Laboratories of the University of Washington at Friday Harbor, under a grant from the American Academy of Arts and Sciences. The writer wishes to express his appreciation to the Academy and to thank the Director of the Laboratories, the members of the staff and in particular Dr. Robert Hungate of Washington State College for their generosity and kind assistance.

# MATERIAL

Worms of the beautiful form *A. fragilis* (Baird), commensal on the locally abundant inter-tidal star *Evasterias troschelii* Stimpson, were selected as the first animals to be used in these experiments and proved a happy choice for a number of reasons. *Evasterias* can be found in large numbers at certain points in Puget Sound where strong tidal currents prevent the deposition of sand or nud or the growth of extensive beds of algae. Stars were collected on a point of Orcas Island on Wasp Passage and on the pilings of the ferry landing at the village of Orcas. Although *Evasterias* has a more local distribution than the ever-present *Pisaster ochraceus*, when concentrations of the animals are found they are often in the same zone and in close association with *Pisaster*, *Pycnopodia*, *Solaster*, *Henricia*, *Leptasterias* appeared to have commensal *Arctonoë*. The original observation of these commensals on hosts in close association with other genera of stars which are not regularly their hosts initiated these experiments.

Large numbers of the mud-star, *Luidia foliolata* (Grube), were collected by dredging in West Sound on the south side of Orcas Island. A high percentage of these stars had commensal *Arctonoë* (*pulchra-fragilis?*). This partnership did

not, however, prove as satisfactory for experimental work as *Evasterias* and its commensal, because of the tendency of the mud-stars to autotomize their arms in the live-boxes and die.

*Stichopus californicus* (Stimpson) with attendant *Arctonoë* (*pulchra-vittata*?) could be collected by dredging or with a long rake almost anywhere in the Sound where there was soft bottom.

Although the large numbers of the form *A. vittata* commensal with the keyhole limpet *Diadora* made this association readily available, the extreme inactivity of these worms was such as to make their use in the experimental apparatus impossible.

It was found that host *Evasterias* and *Stichopus* could be kept in live-boxes for weeks without any apparent effect on the health or activity of their commensals. The worms were found to be extremely hardy and easy to handle. The name *fragilis* is certainly a misnomer and quite clearly the result of the observations of a worker who noticed that the worms break into fractions when placed in formalin or alcohol. In the course of the experiments worms were pulled from the host with forceps, manipulated with camel's-hair brushes, placed in the test apparatus, removed and replaced on their hosts many times without any apparent effect on their health and activity other than the occasional loss of an elytron. Twenty *Evasterias* with commensals were collected at the first of the summer and kept in hive-boxes for two months, and in the tests to be described with *A. fragilis*, their worms were used exclusively. The hosts were fed bivalves of various species and when a star was feeding, its commensal could often be observed lying in the fold between the arms of the star with its head directed toward the everted stomach of the star, apparently stealing a meal.

#### Methods

The essentially simple unit diagrammed in Figure 1 was designed to make commensals choose between two streams of water. It consisted of a glass Y-tube with a seven-and-a-half-inch stem of three-quarter-inch pyrex and two four-inch arms of one-half-inch pyrex at approximately right angles to each other. These arms were extended and bent inward by joining to them three-inch lengths of half-inch pyrex by means of rubber sleeves. This was done in order to eliminate turbulence and to give a smooth flow at the point-of-choice (B). At the open base of the Y-tube (A) was a stop-cock set in a rubber stopper, which could be removed from the Y to allow introduction of animals.

Two identical wooden aquaria with an internal dimension of  $10'' \times 10'' \times 10''$  were each connected to both arms of the Y, making it possible for alternate arms of the Y to be used as test arms. Vents at the bottoms of the aquaria were connected to the extended arms of the Y by  $\frac{3}{16}''$  rubber tubing. By closing a pinch clamp on any one of the four rubber connections, flow in that part of the system could be completely stopped.

Commensals to be tested were separated from their hosts for twelve hours or more prior to an experiment and kept singly in dishes with circulating sea-water, on the theory that by such a procedure the threshold of the worms to "host-factor" might be lowered. Echinoderm hosts were placed in non-circulating, though aerated, sea-water in a glass aquarium and this, in turn, was kept partially immersed in a larger aquarium of circulating sea-water to maintain a low temperature (approxi-

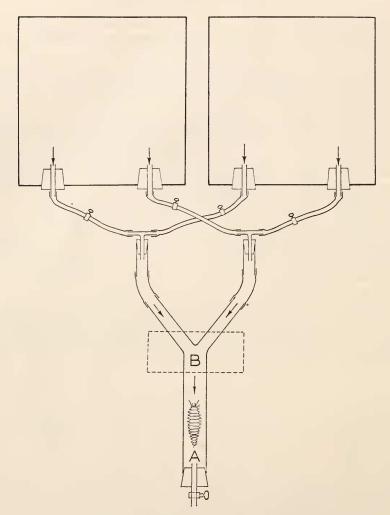


FIGURE 1. Plan of experimental apparatus.

mately  $13.5^{\circ}$  C.) over night. This was done in the hope that "host-factor" might accumulate in the water to be tested. An identical glass aquarium containing seawater alone (or non-host to be tested against host) was treated in a similar manner. Immediately prior to a series of experiments the entire contents of the two glass aquaria including the echinoderms were transferred to the two wooden aquaria of the test apparatus. Each pinch clamp was opened to remove air from the system, both arms of the Y were flushed out from the sea-water or non-host aquarium, and the apparatus was ready for a run.

When a run was to be made, the stopper at A was removed with the four pinch clamps closed, and a worm introduced. The stopper was then replaced and the contained stop-cock opened to allow a slow but constant flow. Two of the pinch clamps were then opened at will to allow water from each aquarium to meet at the point-of-choice (B). When the worm had moved up to the point-of-choice and entered one of the arms of the Y, it was removed from the system, the choice recorded, and the apparatus readied for another run.

Every possible precaution was taken to prevent at the point-of-choice any other imbalance of physical or chemical factors than that desired. The level of water in the two aquaria was kept identical at the beginning of every individual run so that during the run the pressure in the two arms of the Y at the point-of-choice was by necessity equal, the heads above them being equal. The temperature was kept the same in both aquaria  $(13.5-15^{\circ} \text{ C}.)$ .

Before any experiments were made flow tests were conducted using colored indicators. Figure 2 shows the head of a worm at the point-of-choice (Fig. 1, B) with the flow characteristics superimposed upon it. If an indicator was put into one aquarium, it was clearly demonstrated that the flow characteristics were such that if a chemical were to be present in one aquarium, the head of the worm and its tentacles would be asymmetrically stimulated. The two streams did not mix completely at the point-of-choice, there being a region of high concentration of indicator at one



FIGURE 2. Enlargement of Figure 1, B. Flow characteristics as indicated by borax carmine, showing asymmetrical stimulation of tentacles of commensal at point-of-choice.

side, a narrow cone-shaped zone of mixing in the middle and a clear region without indicator at the opposite side. Farther down the stem and at the point of introduction (A) mixing was complete.

In addition, although worms were not strongly or negatively phototactic, in order to control differences in light as well as small differences in temperature, pressure, rate of flow or aeration, in any series of runs water from each aquarium was allowed to flow into alternate arms of the Y. For instance, if a series of runs were being made with a host in one aquarium and sea-water alone in the other, in the first run water from the host flowed into the left arm of the Y, in the next into the right arm, in the next into the left arm again, and so on alternately throughout the series. Between each and every individual run both arms were flushed out from the sca-water (or non-host) aquarium and between any series of tests the whole apparatus was thoroughly washed out with fresh sea-water. Both the glass and wooden aquaria were scrubbed and leached in fresh running sea-water for at least twelve hours. The wooden aquaria used to house hosts during runs were also periodically alternated.

#### OBSERVATIONS

In the data below the total number of times worms were placed in the test apparatus is recorded as the "number of trials." If a worm moved up the stem of the Y and into either arm this is recorded as a "run."

If a worm failed within ten minutes from the time it was placed in the apparatus to reach the point-of-choice or enter either arm of the Y or if it reversed its position, this is recorded as a "failure."

The "negative trials" appearing in some of the tables below equal the sum of "failures" plus "runs into the sea-water (or non-host) arm."

*Experiment No. 1.* Are *Arctonoë fragilis* attracted by sea-water coming from an aquarium containing their host *Evasterias troschelii?* 

No. of trials	43
No. of runs	35
No. of runs into Evasterias arm	33
No. of runs into sea-water arm	2
% runs into Evasterias arm	94.5%
Chi-square of choice (vs. 50/50)	27.4
P	$\ll .01$
No. of failures	8
% failures	18%
No. of worms used	13
No. of worms making five consecutive runs into Evasterias arm	5

It would appear from these data that the worms are attracted by some substance from the host aquarium and that they can distinguish between it and sea-water alone when they reach the point-of-choice.

*Experiment No. 2.* Is the ability of *A. fragilis* to determine which of the two arms of the Y contains sea-water from an *Evasterias* diminished if the other arm contains water from an aquarium containing a starfish of another genus, *Pisaster*, on which the worm is not commensal? Weight *Evasterias*—540 grams. Weight *Pisaster*—430 grams.

No. of trials	36
No. of runs	35
No. of runs into Evasterias arm	33
No. of runs into Pisaster arm	2
% runs into Evasterias arm	94.5%
Chi-square of choice ·	27.4
Р	$\ll .01$
No. of failures	1
% failures	2%
No. of worms used	6
No. of worms making five consecutive runs into Evasterias arm	5

It would appear that the presence of the *Pisaster* in this experiment had no effect on the choice of the worms.

*Experiment No. 3.* What happens if in the above experiment we double the weight of non-host star in the other aquarium? Weight of host-489.5 grams. Weight of two *Pisaster*-866.1 grams.

No. of trials	37
No. of runs	36
No. of runs into Evasterias arm	31
No. of runs into <i>Pisaster</i> arm	5
% runs into Evasterias arm	86.1%
Chi-square of choice	18.68
P	≪ .01
No. of failures	1
% failures	2.7%
No. of worms used	6
No. of worms making five consecutive runs into Evasterias arm	4

It appears that doubling the weight of the non-host *Pisaster* had no significant effect on the ability of the worms to choose the arm of the Y in which water flowed from the host.

Combining all the above data for trials when the host was in the system :

No. of trials	116
No. of runs	106
No. of runs into Evasterias arm	97
No. of runs into sea-water or non-host arm	9
% runs into Evasterias arm	91.4%
Chi-square of choice	73.0
P	$\ll .01$
No. of failures	10
% failures	8.6%
No. of negative trials (9 plus 10)	19
No. of worms used	19
No. of worms making five consecutive runs into <i>Evasterias</i> arm	13

*Experiment No. 4.* How do *Arctonoë fragilis* collected from *Evasterias* behave when their own host is replaced in the test apparatus by a specimen of *Luidia foliolata* which is listed as an occasional host of *A. fragilis? Luidia*—weight approximately 920 grams.

No. of trials	35
No. of runs	14
No. of runs into Luidia arm	8
No. of runs into sea-water arm	6
% runs into Luidia arm	57%
Chi-square of choice	.285
P	.5095
No. of failures	21
% failures	72%
No. of negative trials (6 plus 21)	27
No. of worms used	9

It can be seen from the above that the distribution of runs into the *Luidia* arm and into the sea-water arm does not differ significantly from a chance distribution. Furthermore, if we compare the proportion of the runs into the *Luidia* arm to the negative trials (8/27) with the proportion, taken from the preceding sum of the data when the host was in the system, of the runs into the host arm to the negative trials (97/19), we see that the chi-square is 47.0 and the P  $\ll$  .01. It appears, therefore, that under these experimental conditions at least, *Luidia foliolata* has no attraction for the *A. fragilis* which are commensals of *Evasterias*, in spite of the fact that this worm has been described as occurring on *Luidia*.

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*Experiment No. 5.* Are *Arctonoë* (*pulchra-fragilis?*) attracted by water coming from an aquarium containing their host *Luidia foliolata? Luidia*—weight approx. 920 grams.

No. of trials	35
No. of runs	20
No. of runs into Luidia arm	8
No. of runs into sea-water arm	12
% runs into Luidia arm	40%
Chi-square of choice	.80
P	.3050
No. of failures	15
No. of negative trials (15 plus 12)	27
No. of worms used	8

It appears that the worms cannot discern the presence of their host since the data for choice does not significantly differ from a chance distribution. That the behavior of the worms under these conditions is significantly different from that of worms in which there is evidence of a strong attraction can be seen if we compare the proportions of the number of runs into the host arm to the number of negative trials (8/27) with the same proportion for the sum of the data for *A. fragilis* and *Evasterias troschelii* (97/19). The chi-square is 47.0 and the  $P \ll .01$ .

*Experiment No. 6.* Can the above worms commensal with *Luidia* discern the presence in the system of the star *Evasterias* which has been shown to have a positive attraction for its own commensal *Arctonoë*?

No. of trials	18
No. of runs	5
No. of runs into Evasterias arm	2
No. of runs into sea-water arm	3
No. of failures	13
% failures	72%
No. of negative trials (13 plus 3)	16
No. of worms used	8

The very high proportion of negative trials to total trials (16/18) makes it clear that the substitution of an *Evasterias* for the host *Luidia* in the system has no effect on the behavior of these worms.

*Experiment No. 7.* Are *Arctonoč* (*pulchra-vittata*?) attracted by water coming from an aquarium containing their host *Stichopus californicus*? Host weight approx. 1000 gms.

No. of trials	56
No. of runs	50
No. of runs into Stichopus arm	45
No. of runs into sea-water arm	5
% runs into Stichopus arm	90%
Chi-square of choice	32.0
Р	$\ll .01$
No. of failures	6
% failures	10.7%
No. of negative trials (6 plus 5)	11
No. of worms used	11

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It would appear that these worms can clearly discern the presence of their host and distinguish between host-water and sea-water alone.

*Experiment No. 8.* Are *Arctonoë* commensal with *Stichopus* attracted by water from an aquarium containing another Holothurian, *Cucumaria miniata* (Brandt), found in the same general environment as their host? Combined weight of twelve *Cucumaria* in test aquarium—428 gms.

No. of trials	35
No. of runs	24
No. of runs into Cucumaria arm	9
No. of runs into sea-water arm	15
% runs into Cucumaria arm	37.5%
Chi-square of choice	1.5
Р	.2030
No. of failures	11
% failures	31.5%
No. of negative trials (11 plus 15)	26
No. of worms used	6

It is clear that in this series of runs the distribution beyond the point-of-choice did not significantly differ from a chance one. That the behavior of the worms differed significantly from their behavior when the host was in the system can be seen when we compare the proportion of runs into the *Cucumaria* arm to negative trials (9/26) with the similar proportion from the preceding table when the host was in the system (45/11). The chi-square is 26.2 and the P  $\ll$  .01.

*Experiment No. 9.* What happens if, in the test apparatus, we cross hosts of two partnerships in which a clear attraction has been demonstrated? How do worms commensal with *Stichopus* behave if a specimen of *Evasterias troschelii* replaces their host in the system?

Series A. Evasterias weight approx. 425 grams	
No. of trials	
No. of runs 13	
No. of runs into <i>Evasterias</i> arm 5	
No. of runs into sea-water arm 8	
Chi-square of choice .68	
Р	50
No. of failures 2	
No. of failures 2 No. of worms used 5	
Series B. Evasterias weight approx. 950 grams	
No. of trials 25	
No. of runs 15	
No. of runs into <i>Evasterias</i> arm 11	
No. of runs into sea-water arm 4	
Chi-square of choice 3.2	
Р .05	10
No. of failures 10	
No. of worms used 5	

It can be seen that in both series A and B the distribution beyond the point-ofchoice did not significantly differ from a chance one. Comparing the proportions of the number of runs into each arm in both sets of data we see that in series B in which the weight of *Evasterias* was increased in order to equal more nearly that of the host *Stichopus*, the runs into the *Evasterias* arm were in the majority. However, the number of failures (10) was high for an experiment demonstrating an attraction. A longer series of trials would have to be made in order to determine whether commensals from *Stichopus* may be significantly attracted by water from a large weight of their relative's host, *Evasterias*.

In order to compare the behavior of the worms in these two series of experiments with their behavior when the host was in the system, we may combine the data from series A and B.

No. of trials	40
No. of runs	28
No. of runs into Evasterias arm	16
No. of runs into sea-water arm	12
No. of failures	12
No. of negative trials (12 plus 12)	24
No. of worms used	10

That the behavior of the worms differed from their behavior when the host was in the system can be seen when we compare the proportion of runs into the *Evasterias* arm to negative trials (16/24) with the similar proportion when the host was in the system (45/11). Here the chi-square is 15.7 and the P  $\ll$  .01.

*Experiment No. 10.* How do worms commensal with *Evasterias* behave if a specimen of *Stichopus californicus* replaces their host in the system?:

No. of trials	35
No. of runs	33
No. of runs into Stichopus arm	17
No. of runs into sea-water arm	16
No. of failures	2
% failures	5.6%
No. of negative trials (2 plus 16)	18
No. of worms used	7

It is clear that in this experiment the data of choice did not differ from a chance distribution. That the behavior of the worms differed from their behavior when their host was in the system can be seen when we compare the proportion of runs into the *Stichopus* arm to negative trials (17/18) with the similar proportion from the sum of the data for experiments no. 1, 2 and 3 (97/19). Here the chi-square is 17.6 and the  $P \ll .01$ .

# DISCUSSION

The data above present clear statistical evidence that certain echinoderm hosts produce a specific diffusable substance that acts as a powerful attractant for their polychaete commensals. However, the data cannot describe the characteristic behavior of worms when they are under the influence of the attractant. Tested against sea-water alone, *A. fragilis* showed a random distribution of choice, but 8 of 21 trials were failures, and in the majority of the remainder of the runs the worms were sluggish, took the full ten minutes to reach the point-of-choice, and showed a decided lack of interest in moving up the stem. This behavior was more or less characteristic of all tests when hosts were not in the system and of tests with the mud-star, *Luidia foliolata*. Tested against hosts, however, the characteristic behavior of worms was to hesitate for a brief period at the point of entrance and then suddenly to become activated and move up the stem, waving the head from side to side in searching movements. The delay at the point of entrance appeared in these experiments to be about the same time it took indicator to reach this point in the preliminary flow-tests.

In a number of experiments in which positive results were obtained it is clear that some of the runs into the sea-water or non-host arm were the result of the worm moving so swiftly up the stem of the Y under the influence of "host-factor" that without stopping at the point-of-choice to sample the streams, it simply moved into that arm of the Y nearest the side of the stem to which it was appressed when it reached the point-of-choice. A number of times during the course of the experiments worms were observed to move part way into the sea-water or non-host arm, then pull back and enter the host arm.

The failure of *Arctonoë* commensal with *Luidia* to respond to their own hosts is unexplained. However, it was impossible to obtain an entirely uninjured host for use in the test apparatus and if a whole one was put into the apparatus it soon autotomized one or more arms. Perhaps the failure to obtain a response by commensals depended upon the release of injury substances from these stars.

It would appear that other echinoderms not distantly related to hosts, but without commensals, have no attraction for the commensals. However, a survey of many more forms should be made before this can be certain.

Reciprocal experiments indicate that "host-factor" produced by the host of one partnership has no attraction for commensals of another partnership, in spite of the fact that the commensals may be extremely closely related. However, little light has been cast by these preliminary experiments on the interesting phenomenon of the restriction of what appear to be single commensal species to certain species only of a number of totally unrelated classes of hosts (see Table I). By similar tests it should be possible to give evidence whether or not attractants of two unrelated hosts of the same commensal species may be similar.

It is clearly apparent that details of the life-histories of the forms of the genus *Arctonoë* are needed, involving examination by specialists of extensive series of different age groups of commensals from each of the many host species. Although in the differentiation of the three forms it is almost certain that genetic factors are involved, it would be of great interest to determine whether or not the early stages of one form could be induced to develop on the host of another form and if so, whether morphological as well as physiological adaptations to the new host might occur independent of genetic factors. In certain species of insect parasites, structural polymorphism dependent upon host has been clearly demonstrated by Salt (1937) and others.

That organisms by undergoing their development in contact with certain specific chemical factors may be physiologically conditioned to respond positively to them has been demonstrated by Thorpe (1939) in his work with Drosophila. The work cast some light on earlier observations by Thorpe and Jones (1937) that the wasp *Nemeritis* (Hymenoptera: Ichneumonidae), normally a parasite of the Wax-moth *Ephestia*, could be conditioned to give a positive olfactory response to the Wax-

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moth *Meliphora* if it had undergone its development on this abnormal host. Similar experiments could perhaps be conducted using marine partnerships; they might be initiated by using such forms as the polynoid *Halosydna brevisetosa* Kinberg, in which both free-living individuals and morphologically very different individuals commensal with certain terebellids are readily available. It is quite possible that just as in certain terrestrial host-parasite relationships (Thorpe and Jones, 1937) we have in these intimate marine associations the factor of olfactory conditioning acting as a mechanism of isolation, which Cushing (1941) suggests may be "a physiological factor acting upon population mechanics that does not depend upon genetic changes for changes in its specificity of action."

The general occurrence of chemical factors as controlling agents of hostcommensal relationships in the sea must be surveyed by adapting our apparatus so that members of other phyla can be used, and finally an investigation must be made of the chemical nature of attractants.

## SUMMARY

1. Apparatus was developed which made it possible to determine whether commensals of the polynoid genus *Arctonoë* are attracted by specific substances to their hosts and whether they can distinguish between water coming from an aquarium containing their host and sea-water alone or water from non-host.

2. Arctonoë fragilis (Baird) commensal with the star Evasterias troschelii Stimpson are clearly attracted to their host and can distinguish between water coming from their host and sea-water alone. Arctonoë (pulchra-vittata?) commensal with the cucumber Stichopus are likewise attracted to their host.

3. Arctonoë fragilis commensal with Evasterias are not attracted to the nonhost star, Pisaster, occurring in the same immediate environment as their host. Arctonoë (pulchra-vittata?) commensal with the cucumber Stichopus are likewise not attracted to the non-host Cucumaria.

4. Arctonoë (pulchra-fragilis?) commensal with the mud-star Luidia are not attracted, under these experimental conditions at least, to their own host. Arctonoë fragilis commensal with Evasterias are not attracted to the mud-star Luidia, in spite of the fact that Luidia may be a host of fragilis. These results are perhaps inconclusive, because injury substances may have been released into the apparatus by the mud-stars.

5. Cross experiments (A. fragilis from Evasterias tested against Stichopus and A. pulchra-vittata from Stichopus tested against Evasterias) indicate that attractants released by the two hosts are not the same, since neither commensal is attracted to its relative's host.

#### LITERATURE CITED

BERKELEY, E., AND C. BERKELEY, 1948. Canadian Pacific Fauna, 9. Annelida. 9b (1) Polychaeta Errantia. Fisheries Research Board of Canada, Toronto, 100 pp.

CUSHING, J. E., JR., 1941. An experiment on olfactory conditioning in Drosophila guttifera. Proc. Nat. Acad. Sci., 27: 496-499.

PETTIBONE, MARION H., 1947. Polychaetous annelids of the superfamily Aphroditoidea from the San Juan Archipelago, Puget Sound and adjacent waters. Unpublished doctoral dissertation, University of Washington.

- SALT, GEORGE, 1937. The egg-parasite of *Sialis lutaria*: a study of the influence of the host upon a dimorphic parasite. *Parasitology*, **29**: 539–553.
- THORPE, W. H., 1939. Further studies in pre-imaginal olfactory conditioning in insects. Proc. Roy. Soc. London, Scr. B, 127: 424-433.
- THORPE, W. H., AND F. G. W. JONES, 1937. Olfactory conditioning in a parasitic insect and its relation to the problem of host selection. *Proc. Roy. Soc. London, Ser. B*, 124: 56-81.
- WELSH, JOHN H., 1930. Reversal of phototropism in a parasitic water mite. Biol. Bull., 59: 165-169.
- WELSH, JOHN H., 1931. Specific influence of the host on the light responses of parasitic water mites. *Biol. Bull.*, **61**: 497-499.